

The sections below briefly summarize the topics covered by each of the speakers at the workshop. They are meant to provide general background material and to help workshop attendees focus on the main points of each presentation. Following the workshop, slides from each talk and brief summaries of discussion that ensues in small working groups during the workshop will be posted on the NWFSC web site (<http://research.nwfsc.noaa.gov/cri>).

**I. Identifying populations of Pacific salmonids.** Mary Ruckelshaus and Mike Ford, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA.

Understanding the size and spatial extent of populations is critical for viability analyses that are a necessary step in recovery planning and conservation assessments for any species. The population is the smallest unit for which extinction risk analyses are performed, and the characteristics of the set of populations that constitute a species or Evolutionarily Significant Unit (ESU) determine viability at those larger geographic scales. The definition of a population that we use in this exercise is defined in the Viable Salmonid Population (VSP) document being prepared by NMFS for use in conservation assessments for Pacific salmonids. Portions of the document describing population definitions are excerpted below. (These are excerpted from the draft VSP document—a final review document will be released on or before December 15, 1999. Citations and Appendices referenced below are contained in the draft VSP document.)

**1.1 Population definitions in the VSP document**

A *viable salmonid population* (VSP) is an independent population of any Pacific salmonid (genus *Oncorhynchus*) that has a negligible risk of extinction over a 100-year time frame due to threats from demographic variation (random or directional), local environmental variation, or threats to genetic diversity (random or directional). Other processes contributing to extinction risk (catastrophes and large-scale environmental variation) are also important considerations, but by their nature they need to be assessed at larger temporal and spatial scales represented by collections of populations, such as the scale of ESUs. Goals of the ESA include considering the likelihood of survival and fostering recovery of a listed species in its native ecosystem. These goals can be achieved by assessing the likelihood that a naturally reproducing population will sustain itself into the foreseeable future without continual aid from artificial propagation.

The crux of this definition of a population is what is meant by “independent.” An independent population is any collection of one or more local breeding units whose population dynamics and extinction risk over a 100 year time period are not substantially altered by exchanges of individuals with other populations. In other words, if one independent population were to go extinct, it would not have much impact on the 100-year extinction risk experienced by other independent populations. Independent populations will generally (but not always) be smaller than a whole ESU, and will generally inhabit geographic ranges on the scale of whole river basins or major sub-basins that are relatively isolated from outside migration.

A time scale of 100 years was chosen to represent a “long” time horizon for evaluation of extinction risk. It is necessary to evaluate extinction risk at a long time scale for several reasons. First, many recovery actions (such as habitat restoration) are likely to have effects on population status at a long time scale. Second, many genetic processes important to understanding population function, such as the loss of genetic diversity or accumulation of deleterious

mutations, occur at long time scales and current actions can affect these processes for a long time to come. Third, at least some environmental cycles occur over decadal or longer time scales (e.g., oceanic cycles--Beamish and Bouillon 1993, Mantua et al. 1998, Hare et al. 1999), and in order to evaluate a population's status it is important to anticipate far enough into the future to be able to accommodate large-scale environmental oscillations or trends.

*Definition of a population that NMFS will use in applying the VSP concept*

For application of the VSP concept, NMFS defines an independent population following Ricker's (1972) definition of a "stock": an independent population is a group of fish of the same species spawning in a particular lake or stream (or portion thereof) at a particular season which to a substantial degree does not interbreed with fish from any other group spawning in a different place or in the same place at a different season. For our purposes, not interbreeding to a "substantial degree" means that two groups will be considered to be independent populations if they are isolated to such an extent that exchanges of individuals among the populations do not appreciably affect the population dynamics or extinction risk of the independent populations over a 100-year time frame. The exact level of reproductive isolation that is required for a population to have substantially independent dynamics is not well understood, but some theoretical work suggest that substantial independence will occur when the proportion of a population that consists of migrants is less than about 10% (Hastings 1993). This definition identifies independent populations as units about which it is biologically meaningful to evaluate and discuss the extinction risk due to intrinsic factors such as demographic, genetic or local environmental stochasticity of one population independently from other populations.

The degree to which a group of fish has dynamics that are independent from another group depends in part on the relative numbers of fish in the two groups. Ten migrants into a group of 1,000 fish will have a much smaller demographic impact than 10 migrants into a group of 10 fish. Practically speaking, applying the definition of a population as described in this document will involve making an assumption about the expected degree of independence of groups of fish under historical or "natural" conditions (i.e., before the recent or severe declines that have been observed in many streams.) As long as the relative proportions of fish in two groups can be assumed to be representative of what they were under historical (pre-decline) conditions, evaluation of the degree to which their dynamics are independent will be informative. It is necessary to consider historical conditions so that a definition of a population is not contingent on the relative conservation status of groups of fish (i.e., so that cases where the degree to which one group of fish is isolated from another is completely dependent on the relative abundances of the two groups.) In some cases it may be determined that environmental conditions are so altered that it is either impossible to evaluate the pre-decline population structure of an ESU or that the population structure of the recovered ESU will be substantially different from what it was historically. In these cases it may be necessary to identify both the current population structure and what the population structure is expected to be after recovery has been achieved.

The Washington Department of Fish and Wildlife (WDF 1993) and the Oregon Department of Fish and Wildlife (OAR 635-07-501(38)) both use population definitions that involve some level of reproductive isolation among populations. This focus on demographic independence in defining populations is consistent with how the population concept is often applied in fisheries analysis. Estimation of spawner/recruitment relationships is a common analytical tool in fisheries biology. For these analyses to be applicable, particularly where

density dependence in reproduction is involved, populations must be assumed to be reproductively isolated. Indeed, inadvertently pooling groups of fish from different independent populations is a major source of error in estimating spawner/recruit relationships (Hilborn and Walters 1992, Ray and Hastings 1996). Whether explicitly stated or not, most analyses using spawner/recruit relationships are assuming a population (or “stock”) definition similar to the one used in this paper.

#### *Distinction between Population Definition and Tools for Estimation*

In Appendix #, we describe several ways to estimate dispersal rates and population boundaries. These include mark-recapture studies, exploring correlations in abundance time series, assessing patterns of phenotypic variation, and using molecular genetic markers to track individuals or estimate similarity among groups of fish. We believe the following types of data will be useful in gaining insight into the degree of reproductive isolation among spawners in different areas: (1) patterns of allele frequencies, (2) correlations in abundance over time, (3) geographic and temporal spawning distributions, (4) mark/recapture data, and (5) physical data about the environments inhabited by the fish. Allele frequency data can be used to test models of population structure and to estimate migration rates among groups. Abundance correlations can be used to directly test for demographic correlations. Geographic and temporal spawning distributions can be used to make judgements on the likelihood of movement among areas. Mark/recapture data can provide direct estimates of straying, and environmental data can be used to make judgements on the likelihood of local adaptations among groups. It is important to emphasize that these techniques are simply tools for estimating population boundaries, and they are not part of the population definition itself. For example, patterns of molecular genetic markers may provide good evidence of the degree of reproductive isolation between groups of fish. However, our definition of a population does not in any way stipulate how to interpret the genetic patterns. As a case in point, identification of statistically detectable differences in allele frequencies does not automatically necessitate designation of separate populations as defined here.

Just as molecular markers are one tool for determining population boundaries, geographic characteristics also may be used to help identify populations. Spatial distributions of spawning groups and whole salmonid populations will be constrained by geographical features such as basin and sub-basin structure. Physical locations of suitable habitats within a basin and the dispersal capabilities of the fish will combine to determine in part over how large an area fish within a population will be distributed. We emphasize that populations cannot be defined based on geography (they are defined based on biological processes; i.e. reproductive isolation and independent extinction risk). Biology may dictate that a population’s geographic boundaries occur at scales smaller or larger than a single basin or sub-basin (however defined). Given seven species and many life history variants, the geographic expanse occupied by different populations is likely to vary substantially. An example of how one might use such data to identify populations is given in Appendix #.

#### *Structure below and above population level*

A population is described as a group of fish that is reproductively isolated “to a substantial degree.” As a criterion for defining groups of fish, the degree of reproductive isolation is a relative measure, however, and can vary continuously from the level of pairs of fish to the degree of reproductive isolation separating species. The “population” defined here is not,

therefore, the only biologically logical grouping that can be constructed. Below the level of the population, for example, there will often be groups of fish that are to some degree reproductively isolated from other groups of fish within the population, but are not sufficiently isolated to be considered independent by the criteria adopted here. These groups of fish are referred to as “subpopulations.” As will be described, the existence and interaction of subpopulations can have important consequences for characterizing a VSP, and population spatial structure is proposed as one of four key parameters for evaluating the status of a population.

Just as there may be substructuring within a population, there may be structure above the level of a population. This is explicitly recognized in the designation of an ESU. An ESU may contain multiple populations that are connected by some small degree of migration. Thus organisms can be grouped in a hierarchical system where we define the levels of individual, subpopulation, population, ESU and finally species. Other hierarchical systems with more or fewer levels could be constructed. Though reproductive isolation forms a continuum, it is probably not a smooth continuum, and there exists a biological basis for designating a hierarchy of subpopulations, populations and ESUs.

## **1.2 Identifying populations—early applications to Pacific salmonid ESUs**

Population structure of spring-run chinook salmon and steelhead in the Upper Columbia River ESUs has been identified by a work group of comanagers and Federal scientists convened as part of an effort to provide a "Quantitative Analytical Report" on the effects of the Columbia River hydrosystem on listed Upper Columbia River spring chinook salmon and steelhead. The populations were identified and then became the conservation units for which interim recovery goals were developed. A similar exercise is underway for the chinook salmon in the Puget Sound ESU, although this effort is in its early stages. Data that are available and analyses performed as part of identifying populations of salmonids will be discussed for both of these geographic regions as a way of illustrating possible approaches to this challenging problem. It is our hope that discussion at this workshop will spur further research and data collection efforts aimed at identifying populations of Pacific salmonids and other species of conservation concern.

## **II. Population structure considerations in assessing viability of salmonids.** Chris Ray, University of Nevada at Reno.

The answer to the question 'How many and which populations are necessary to maintain the viability of an ESU?' depends on how well we can predict population dynamics within the ESU. An appropriate model of population dynamics allows us to predict persistence, the maintenance of genetic diversity and the impacts of different management strategies. Building a predictive model requires explaining the variance in demographic rates caused by fluctuations in the natural environment, density effects and management. Without an explanation of the variance in demographic rates, we must resort to 'rules of thumb' to predict the viability of an ESU. These rules can be drawn from general population or metapopulation theory, with support from selected empirical studies. Current theory falls somewhat short of providing rules of thumb for the successful management of spatially complex populations like salmonids. The predictions of general models of persistence and the maintenance of genetic variation are very sensitive to the scale of population processes like density dependence, local extinction and population mixing. I offer examples of this sensitivity from theoretical studies and from a population viability analysis currently under development for Lahontan cutthroat trout. Successful salmonid management will require answering several difficult questions about population dynamics, including: How independent are populations demographically? Genetically? Environmentally? At what spatial scales does population density affect each age class? This workshop would be the place to develop a list of such questions that must be answered before management can commence.

**III. Can simplistic, spatially explicit models be useful for evaluating the demographic and genetic structure of salmonid populations?** Chris Jordan, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA.

MODELS OF SALMON BIOLOGY

Mathematical models in biology are predictive tools subject to successive refinements. Due to the inherent complexity of the natural world, all models must involve simplifications and assumptions. Thus the question of evaluating biological models becomes one of how damaging are these simplifications and assumptions and what can the model say about reality despite the simplifications?

As a result, the systems to which mathematical modeling tools are successfully applied are ones in which there is considerable biological data, or conveniently the simplifying assumptions accurately represent the biological system in question. Unfortunately, much of the fundamental biology of Pacific salmonid species is not well known, primarily due to the enormous complexity of these animal's natural history. Salmon species as a whole have highly variable life-history strategies. Single species occupy very large geographic ranges covering multiple habitat types over long generation times. Additionally, these species are subject to many sources of natural and unnatural mortality and many human-induced alterations to their environment. From a modeling perspective, this complexity and spatial extent and variability of makes any model very difficult to parameterize. Thus I would consider salmonids to be amongst the worst possible choice of biological systems to model.

Without realistic parameters, or even the basic understanding of what the parameters are and what they look like, how can we believe what a model of salmon biology says? Perhaps we can't, but what we can believe is how models inform our understanding of the biological processes that govern the ecology of salmonid species. So, rather than looking to models for all of the answers, at this point (due to our level of understanding of the biology of these organisms) models should be used for rapid assessment of risk factors, determining criticality of risk factors and testing our understanding of salmonid biology.

I am developing a series of mathematical models to be used in this manner to assess the risk factors in Pacific salmon species. This work is part of the initial phases of recovery planning for the recently listed salmonid ESU's. Fundamental to these recovery plans is some sort of decision support system. Predictive models will play a large role in the framework of the decision support system, since it will rarely be feasible to undertake biological experiments on the time frame of the recovery decision process.

A SIMPLISTIC MODEL OF SPATIALLY STRUCTURED 'SALMONID' POPULATIONS

*What the model is:*

This model is a spatially explicit population dynamical representation of a group of salmonid breeding locales. The basic form of the model is similar to a classic meta-population, where individual sub-populations are coupled to varying degrees, and the entire population's dynamics emerges from the aggregate behavior of the individual populations. It is not clear if salmonids are true meta-populations, but for convenience I adopt the nomenclature.

In the model the breeding areas, or reaches, are located on a branching tree to represent a system of tributaries in a drainage. The spatial scale is not specified, nor is the geometry of the

areas between branches. Instead I only specify the number and order of branches and presence or absence of a breeding area between successive branchings.

The biology of the populations in the model is similar to OR/WA Coho: single reproductive event, non-overlapping generations, single overwintering in freshwater, an ocean life phase and high natal site fidelity. The model follows individual breeding areas in space, and the cohorts that result from these reaches.

Each cohort is subject to mortality at each stage in the life cycle. Mortality is included in the model in a manner similar to matrix models in that life stage transitions are subject to transition probabilities. The resulting sources of mortality are: ocean survival and migration-phase survival. The population dynamics are also influenced by environmental variability (extrinsic density independent mortality). The biological processes that are affected by environmental variability are fecundity and ocean survival. The environmental variability is driven by long period (10 generations) cycles mimicking decadal ocean productivity cycles. Each reach is also subjected to catastrophic loss of productivity with a small probability. In addition, there is natural variation (intrinsic) in the mean fecundity of a population in each reach. The only aspect of the population dynamics that is density dependent is the overwinter survival of the in-stream juveniles. Thus, the model tracks individual cohorts as they progress through the life cycle from eggs to spawning adults.

The spatial structure comes into play in that there is not complete natal-site fidelity. To represent straying the population from each reach has a finite, although sometimes very small, probability of ending up in all of the other reaches. Therefore, all reaches are potentially demographically coupled through straying. I determine the matrix of straying probabilities by thinking of the branching structure of the reaches as a series of choices that the migrating individual must make. I set the probability of making the correct choice and simulate the resulting distribution conditional to the fact that once a wrong choice has been made (wrong turn at a branch, or continuing past the correct reach) all further outcomes are equally possible (choices at branches, stopping or proceeding at subsequent reaches). Although this may be a somewhat simplistic view of migration, it does allow me to manipulate a large component of the meta-population dynamics with a single parameter, the probability of making the correct choice at all branches.

In addition to tracking the population dynamics of each reach, I also track genetic markers in each cohort. I assume that I can identify 10 loci, each with 10 possible alleles in all populations. These loci are not subject to mutation or selection, but are inherited and are subject to drift due to small breeding population size and small number of strays. I initiate the simulations with each reach uniquely determined genetically, and track their relative isolation through time with Nei's allele frequency based metric of genetic distance.

The model is run for 100 generations, and replicated 100 times. All reported values are means (and standard deviations) across the replicates.

#### *What the model isn't:*

The model lacks the spatial detail of a GIS-type spatial model where habitat information is included on a scale finer than that of the breeding reach or where habitat quality distant from the breeding reach can influence the population dynamics. The model has little or no density dependence. It is not based on a Ricker style stock-recruitment dynamic. The model is not individual based, rather it tracks the size of individual populations and their projected genetic structure.

## SO WHAT GOOD IS IT?

Obviously the model, though somewhat complex, is a gross simplification of the biological, spatial and dynamical properties of salmonids, but it captures what is generally considered to be the major features that drive patterns of population persistence and extinction. To be of use in decision support for salmonid population management, the model must predict the dynamical consequences of imposed actions. In the case of a model population, management actions are nothing more than directed parameter variation. I assess the impact of parameter variation by reporting two features of subpopulation dynamics: mean time to quasi-extinction, and genetic isolation.



**IV. Effects of spatial structure and connectivity on coho salmon population dynamics.**  
Peter Lawson, National Marine Fisheries Service, Northwest Fisheries Science Center, Newport  
OR.

**V. Spatial and habitat criteria for salmon recovery planning: hedging bets on the craps table of extinction.** Chris Frissell, University of Montana, Flathead Lake Biological Station.

In addition to the draft report included below, Dr. Frissell included two additional references as background material for the information presented in his talk.

1. Frissell, C. A. and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. *Journal of the American Water Resources Association*. 32: 229-240.
2. Frissell, C. A. 1997. Ecological principles. Pp. 96-115 In: J. E. Williams, C. A. Wood and M. P. Dombeck (Eds.) *Watershed Restoration: Principles and Practices*. American Fisheries Society, Bethesda, MD.

**VI. Catastrophic Risks and Recovery Goals.** Paul McElhany, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA.

The following are excerpts from a working draft of the VSP (Viable Salmonid Populations) paper. A complete draft of the VSP paper will be available for public comment on Monday, December 13. The paper is still in revision and the draft released on December 13 may differ from this workshop document.

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**ESU Viability** (From main body of VSP document)

**Introduction**

To help understand basic salmonid biology and formulate priorities for salmon management, it is useful to explore the extinction risks that individual populations experience. However, in many cases it is also important to consider how these individual population risks relate to sustainability of larger conservation units such as Genetic Diversity Management Units, Major Ancestral Lineages (WDFW), or Gene Conservation Groups (ODFW). The ESA is ultimately concerned with the extinction of any entity that qualifies as a "species" under the ESA, which for vertebrate animals includes species, subspecies, or "distinct population segments." According to NMFS policy, groups of salmon populations that represent Evolutionarily Significant Units (ESUs) of the species as a whole are considered distinct population segments and hence, "species" under the ESA. The goal of this section of the paper is to discuss factors that should be evaluated when determining the numbers and distribution needed to sustain larger conservation units such as ESUs. Like the the section on population viability, this section describes only qualitative guidelines for determining ESU viability. The assumption is that in order to determine the necessary population numbers and distribution in a given ESU, case-specific information will be required. Appendix # provides a more detailed rationale for the guidelines.

**Number and distribution of populations in a recovered ESU**

By definition, a VSP has a negligible risk—a time scale of 100 years—of going extinct as a result of genetic change, demographic stochasticity, or normal levels of environmental variability. If these were the only factors influencing viability, a single VSP would be enough to ensure the survival of an entire ESU. However, three additional factors need to be considered in relating VSPs to viable ESUs: (1) Catastrophic events, (2) long-term demographic processes, and (3) long-term evolutionary potential. Catastrophic events are sudden, rare occurrences that severely reduce or eliminate an entire population. These events fall outside the scope of the "normal" temporal and spatial scales of environmental variation considered when evaluating VSPs. Long-term demographic processes involve extinction and recolonization of entire populations at time scales greater than 100 years. The concern about long-term evolutionary potential centers on the role diversity plays in ESU viability over time scales that are generally greater than 100 years.

In addition to biological considerations, the ESA defines an endangered species as a

species that is “...in danger of extinction in all or a significant portion of its range.” The ESA does not define “significant portion of the range” and there is no indication that the phrase is meant to be (or can be) defined entirely in scientific terms. As Appendix # notes, it will probably be necessary to define “a significant portion of the range” in both scientific and policy terms. Scientifically, a significant portion of the range will be determined by evaluating the risks to ESU persistence at a number of time scales—including those longer than 100 years.

### **ESU Viability Guidelines**

**1. ESUs should contain multiple populations.** If an ESU is made up of multiple populations, it is less likely that a single catastrophic event will cause it to become extinct. Also, ESUs may function as “metapopulations” over the long term and the existence of multiple populations allows for ESU-level extinction/recolonization processes which, in turn, may increase ESU viability. In addition, multiple populations within an ESU increase the likelihood that a diversity of phenotypic and genotypic characteristics will be maintained, thus allowing natural evolutionary processes to operate and increasing the ESU’s viability in the long term. Obviously, this guideline does not apply to ESUs that contain a single population (e.g. Lake Ozette sockeye). In ESUs containing a single population, Guideline 6 becomes increasingly important.

**2. Populations in an ESU should be geographically widespread.** Spatially correlated environmental catastrophes are less likely to drive a widespread ESU to extinction. This guideline also directly relates to the ESA mandate of protecting a species in a “significant portion of [its] range.”

**3. Populations should be geographically close to each other.** On long temporal scales, ESUs may function as “metapopulations” and having populations geographically close to one another facilitates connectivity among existing populations. Thus, a viable ESU requires both widespread (Guideline 2) AND spatially close populations.

**4. Populations should not all share common catastrophic risks.** An ESU containing populations that do not share common catastrophic risks is less likely to be driven to extinction by correlated environmental catastrophes. Maintaining geographically widespread populations is one way to reduce risk associated with correlated catastrophes (Guideline 2), but spatial proximity is not the only reason why two populations could experience a correlated catastrophic risk.

**5. Populations that display diverse life-histories and phenotypes should be maintained.** When an ESU’s populations each have a fair degree of life history diversity (or other phenotypic diversity), it is less likely to go extinct as a result of correlated environmental catastrophes or changes in environmental conditions that occur too rapidly for an evolutionary response. In addition—assuming phenotypic diversity is caused at least in part by genetic diversity—maintaining diversity allows natural evolutionary processes to operate within an ESU. Note that to protect genetic diversity, it may be necessary to maintain several populations with the same phenotype (see Guideline 1).

**6. Some populations should exceed VSP guidelines.** Larger and more productive (“resilient”) populations may be able to recover from a catastrophic event that would cause the extinction of a smaller population. An ESU that contains some populations in excess of VSP threshold criteria for abundance and productivity is less likely to go extinct in response to a single catastrophic event that affects all populations. It is important to note that the abundance guidelines do not take catastrophes into account. This guideline is particularly relevant if an ESU consists of a single population.

**7. Evaluations of ESU status should take into account uncertainty about ESU-level processes.** Our understanding of ESU-level spatial and temporal process is very limited. ESUs are believed to have been historically self-sustaining and the historical number and distribution of populations serves as a useful “default” goal in maintaining viable ESUs.

## **Catastrophes** (From Appendix A.8 of VSP document)

We define catastrophic events as those that cause a severe, sudden reduction in or elimination of an entire population. For the purposes of this discussion “severe” reductions involve elimination of more than 75% of the breeding adults. By “sudden”, we are defining events that happen within a single season, though the impact on adults may not be observed until several seasons after the event. Events that unfold over a longer time span will be discussed in the sections on long-term demographics and evolution. It should be noted that environmental events form a continuum from catastrophes to the “normal” environmental variation considered in VSP analysis. Our choice of 75% reduction of a breeding population is an arbitrary definition of severe that can be modified to reflect the dynamics of a particular population or ESU. Historically, natural catastrophes that affect entire populations were probably rare events at the 100-year time scale, at least in the central portions of the species range (Bisson et al. 1997), but human activity may cause some populations to have a high current risk of extinction from catastrophes within a 100-year time scale.

We considered the effects of catastrophes at the ESU level rather than at the individual population level for three reasons. 1) Because of their potential to affect large as well as small populations, catastrophes can be qualitatively different from the stochastic processes considered for evaluating VSPs. 2) Concerns about catastrophic risk may extend beyond the 100 year time scale used to evaluate VSPs. 3) Catastrophic events can affect more than one population at a time, making it appropriate to evaluate catastrophic risk at the ESU-level. Although we are discussing catastrophes at the level of the ESU, it will generally be necessary to evaluate the catastrophic risk of individual populations, and then integrate this information in an assessment of the overall status of the ESU. We have not developed any specific guidelines for evaluating the catastrophic risk to individual populations, though such guidelines would be valuable.

Catastrophic events may be of natural or anthropogenic origin, or may result from the interaction of the two. Natural catastrophes include volcanoes, earthquakes, disease epidemics, extreme weather, landslides, and unusual fires. Anthropogenic catastrophes include oil and chemical spills, water diversion/dam failures, and major miscalculations in harvest plans. Catastrophes may also result from the interaction of natural and anthropogenic effects. For example, a rain storm that would have little affect on a salmonid population under pristine conditions could become a catastrophe in a heavily modified landscape that has been clear-cut or intensively urbanized. Thus, human activities can increase the frequency of some types of catastrophic events, like floods. Bisson et al. (1997) list different types of natural and anthropogenic disturbances affecting salmon populations and attempt to estimate the frequency of each.

Catastrophes can have profound effects on risks of extinction, and models predict that the rate and severity of catastrophes can be the most important factor in determining the risk of extinction for a population (Lande 1993, Mangel and Tier 1994, Menges 1990). For example, the recovery plan for the federally listed Southern sea otter in California identified catastrophic oil spills as the primary risk to population viability, and recovery goals were based on quantitative estimates of risk of this type of catastrophe (Ralls et. al. 1996). Given the number of potential catastrophic threats facing salmonid populations, in many situations we would expect catastrophes to have a substantial influence on extinction risk, and most of the guidelines regarding ESU viability focus on catastrophic risk.

**SimSalmon** (Note: This is not from the VSP paper, but was written as workshop material.)

SimSalmon is a computer simulation program to estimate extinction risk for salmonids. The model used in the program explicitly incorporates the age structure of the population, which provides an advantage over other methods used to estimate extinction risk (e.g. Dennis et al. 1991). Like the Dennis model, SimSalmon has very few parameters and they can be estimated using a time series of abundance plus an estimate of spawner age structure. The program is still in development, but should be publicly available in early 2000. A thorough analysis of the program output as applied to real data and a comparison to other extinction risk models is planned. The following is simply a short description of the model, with a discussion of how the model can be used to explore the effects of catastrophic events.

The model is based on the simple equation

$$N_t = \sum_{i=1}^{\text{max. age}} N_{t-i} R_{t-i} A_i,$$

where  $N_x$  is the number of spawners at time  $x$ ,  $R_x$  is the spawners per spawner at time  $x$ ,  $A_i$  is the average proportion of spawners that are age  $i$  and maxAge is the maximum age at maturation. The spawner per spawner parameter,  $R_x$ , is a random variable that introduces environmental stochasticity into the model. In the simplest formulation,  $R$  is assumed to be distributed lognormally and the two shape parameters of the distribution can be estimated from a time series of abundance. More complex scenarios involving temporal autocorrelation in  $R$  can also be tested, though obtaining autocorrelation parameter estimates from data can be challenging.

The basic simulation protocol involves choosing an initial number of spawners for years one through maxAge. The number of spawners is then projected forward in time by looping through the equation above. This process is repeated 100's or 1,000's of times and the proportion of population trajectories that go extinct by a given period of time is reported as the probability of extinction for that time horizon.

The model utilizes a user specified depensation threshold (henceforth, "threshold"). If the number of spawners drops below the threshold, the recruitment,  $R$ , is zero for that year. Although recruitment for a given year may be zero, it does not mean that the population is necessarily extinct. There may still be individuals out in the ocean that will return to spawn the next year. A population is only considered extinct if there are zero spawners over a number of sequential years equal to maxAge. Thus, the depensation threshold is not equivalent to the "quasi-extinction" threshold of Dennis type models.

Density dependence is currently incorporated into the model as an optional ceiling on the total number of spawners. If  $N > K$ , then set  $N = K$ , where  $K$  is the carrying capacity or ceiling.

Confidence intervals can be determined for the extinction risk estimate by bootstrapping using a method analogous to that used in Dennis et al. It is easiest to work with  $\ln(\text{spawners/spawner})$  rather than  $R$ . Since  $R$  is lognormal, the distribution of  $\ln(\text{spawners/spawner})$  is normal. The mean,  $\mu$ , and variance,  $\sigma^2$  for  $\ln(\text{spawners/spawner})$  are related to the mean,  $\omega$ , and variance,  $\psi^2$ , of the lognormally distributed  $R$  as follows,

$$\begin{aligned} \mu &= e^{\left(\omega + \frac{\psi^2}{2}\right)}, \\ \sigma^2 &= (e^\omega)^2 * e^{\psi^2} * (e^{\psi^2} - 1). \end{aligned}$$

The mean of the  $\ln(\text{spanwers/spawner})$ ,  $\mu$ , is distributed as

$$N\left(m, \frac{s}{\sqrt{sampleSize}}\right).$$

The variance of  $\ln(\text{spawners}/\text{spawner})$ ,  $\sigma^2$ , is distributed as

$$Chi(sampleSize - 1) * \frac{s^2}{(sampleSize - 1)}.$$

By taking repeated, independent draws from these distributions, then recalculating the extinction risk [after converting from  $\ln(\text{spawner}/\text{spawner})$  back to  $R$ ], it is possible to obtain a distribution for the extinction risk. From the distribution of extinction risk, any desired confidence interval can be determined.

### **SimSalmon and Catastrophes**

Using SimSalmon, I explored the consequence of single or sequential years of reproductive failure imposed on a fairly large population. Complete reproductive failure in a large population could occur as the result of a catastrophic event. For example, a drought or water diversion failure could completely dewater a stream for one or several years. While such an event would be extremely alarming, it is not clear how such an event would impact overall viability of a salmonid population. For many species (i.e., chinook, steelhead, sockeye, cutthroat, chum, some coho), individuals do not all mature at the same time. As a result, not all individuals return to spawn at the same time, and if reproductive failure occurs in one year, there may still be individuals in the ocean that can return to spawn in a later years. There is thus a spatial and temporal buffering in the effects of catastrophic events on population viability.

To examine the importance of this buffering, the SimSalmon model was run using different initial population sizes. The parameters used in the model were mean  $R = 1$ , variance in  $R = 1.72$ , depensation threshold = 10, and no ceiling was imposed. The age distribution from a lower Columbia River chinook population was arbitrarily chosen to use in this example (Table 1). The initial population sizes are shown in Table 2.

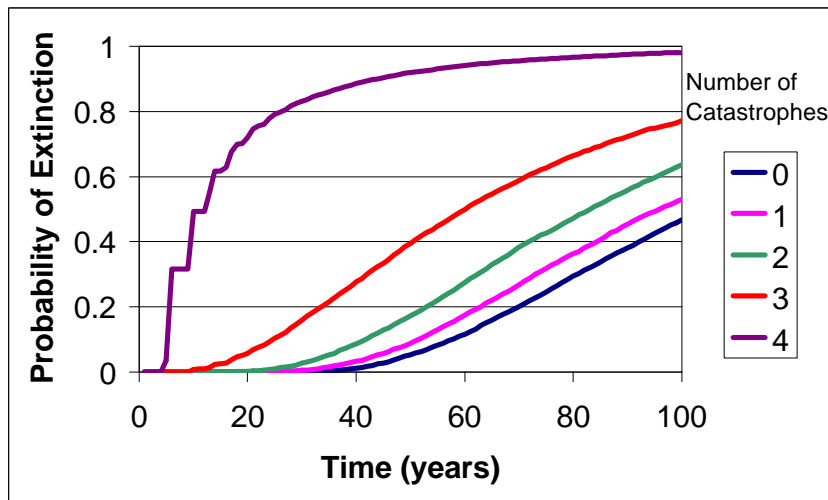
Table 1: Age distribution of lower Columbia chinook.

Age	1	2	3	4	5
Proportion	0	0.05	0.39	0.54	0.02

Table 2: Initial population sizes used to explore effect of catastrophes.

Year	Number of Sequential Years of Catastrophic Reproductive Failure				
	0	1	2	3	4
1	5000	5000	5000	5000	5000
2	5000	5000	5000	5000	0
3	5000	5000	5000	0	0
4	5000	5000	0	0	0
5	5000	0	0	0	0

A catastrophe is simulated as zero spawners in the initial population distribution. Results from these simulation runs are shown in Figure 1.



**Figure 1:** Estimates of extinction risk for simulated populations experiencing various numbers of sequential catastrophic failures in reproduction.

The impact of the number of years over which a catastrophe occurs is very non-linear. A single catastrophic failure does not have a large impact on extinction risk in this scenario. The risk of extinction increases substantially as the number of years of catastrophe increases. The low increase in risk associated with a single year event suggests that the temporal and spatial buffering created by the salmonid life-history will reduce the risk of catastrophes for large populations.

The research presented at this workshop is only intended to demonstrate an approach for understanding how salmonid life-history affects catastrophic risks. A more complete analysis of this question is currently underway.

**VII. Integrating population biology, landscape patterns, and viability analyses into habitat conservation planning for the Florida scrub-jay.** Reed Bowman, Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862.

The Florida scrub-jay (*Aphelocoma coerluscens*) is the only bird species endemic to Florida. Within the last 50 years, habitat loss and degradation have reduced its numbers by 85%. It is completely or functionally extirpated from substantial portions of its former range, and the species continues to decline. The Florida scrub-jay is federally listed as Threatened, thus the USFWS convened a Recovery Team to develop a conservation plan to halt the decline of this species. The overall goal of the Recovery Team has been to maintain stable populations of Florida scrub-jays throughout their current distribution and to maintain, to the extent still possible, the genetic, behavioral, and ecological integrity of natural subpopulations of scrub-jays, and their ecosystem, *in situ*. Because the Florida scrub-jay is a habitat specialist requiring large areas of native, fire-maintained oak scrub, it is best protected by establishing a network of well-managed habitat preserves. The Florida scrub-jay Recovery Team is using data on the distribution, demography and dispersal patterns of scrub-jays in a variety of landscape contexts to develop biological guidelines for establishing a network of reserves and these same data to develop stage-based individual and spatially-explicit population models to assess viability of scrub-jays in a variety of different reserve networks and landscape mosaics.

We mapped the state-wide distribution of the Florida scrub-jay by documenting their occurrence and numbers and the condition of their habitat throughout their current range. We used dispersal distance distribution curves and the proportion of suitable habitat patches occupied by scrub-jays as a function of their distance to the nearest occupied patch to determine the relative isolation of occupied patches. Based on these data and field observations, we chose 3.5 km to delineate subpopulations and 12 km to delineate metapopulations. We delineated 191 different subpopulations and 42 different metapopulations. Of the 42 metapopulations, only three consisted of more than 400 breeding pairs of scrub-jays, comprising over half of all remaining pairs; 21 consisted of fewer than 10 breeding pairs. Individual, stage-based, stochastic population models suggest 400 breeding pairs is necessary to reduce the probability of extinction to less than 1% over 100 years. Because of the obvious importance of these large populations to long-term persistence of the species, we established 400 pairs as the minimum population size allowable for the three core populations.

We also identified five geographic regions which represent remnants of once nearly contiguous habitat. Soils maps and genetic analyses suggest that even before human modification of habitats, these regions may have been separated by habitat unsuitable for Florida scrub-jays. These gaps have been further widened by anthropogenic changes. Each of the three core populations (> 400 pairs) occur in a different geographic region, but in two regions few if any large jay metapopulations exist. In addition, some scrubs occupied by jays are located on geographically-distinct formations separate from the five aforementioned regions. Because of the importance of maintaining genetic integrity of scrub-jays, we sought to establish persistent populations in each region and these peripheral areas.

The spatial structure and landscape mosaic varied greatly between metapopulations. We used a spatially-explicit, individual-based model developed specifically for the Florida scrub-jay to examine the viability of each metapopulation, to ask questions about the amount and spatial pattern of future land acquisitions, and to establish priorities for both land acquisition and



management. The model incorporated demographic stochasticity, environmental stochasticity, epidemics, and other details of scrub-jay biology simulated on realistic landscapes derived from satellite imagery. We ran a series of simulations for each metapopulation based on different reserve designs. These ranged from a simulation of the extant jay distribution assuming no further acquisition to one assuming all potentially-suitable land was acquired and populated with scrub-jays. Various intermediate acquisition scenarios alternately emphasized habitat connectivity or habitat contiguity. Model outputs included percent population decline and probabilities of extinction and quasi-extinction over a 60 year period. From model outputs, we had the basis for ranking the vulnerability of metapopulations and the future restoration potential of each. By adding or deleting individual patches within metapopulations, we were able to evaluate the relative importance of each patch by examining the proportional change in model outputs.

**VIII. Distinct population segments and recovery criteria for spectacled eider and Steller's eider, two ESA-listed species.** Paul Wade, NOAA National Marine Mammal Laboratory, Seattle, WA.